A new species of *Columbella* (Neogastropoda: Columbellidae) from the Caribbean Neogene

Marta J. deMaintenon
Department of Marine Science
University of Hawaii at Hilo
200 W. Kawili Street
Hilo, HI 96720 USA
demainte@hawaii.edu

ABSTRACT

A new species of *Columbella* is described from the Neogene of the southwestern Caribbean and compared with other Caribbean *Columbella* species. The new species is a member of a species pair differing primarily in inferred larval ecology. Protoconch morphology suggests that the new species had planktic development, whereas its extant analogue, *Columbella mercatoria* (Linnaeus, 1758), has nonplanktic development. Though the 2 species were contemporaneous, they do not appear to have been sympatric.

Key words: Colombia, Costa Rica, larval ecology, protoconch.

INTRODUCTION

Evolutionary divergence in larval ecology between planktic and nonplanktic modes is a common pattern in marine molluscs. Many gastropod genera in several families display both reproductive modes. Recent evolutionary divergence may result in pairs of species differing primarily in larval shell morphology. Traditionally, such variation was considered as evidence for poecilogony, intraspecific variation in larval developmental modes. Recent reviews of poecilogony in marine invertebrates (Hoagland and Robertson, 1988; Bouchet, 1989; Knowlton, 1993; Oliverio, 1996) however, have found little evidence to definitively support that poecilogony occurs. Hoagland and Robertson (1988) reviewed reported cases of poecilogony in marine gastropods, and concluded that the pattern of larval development is generally informative in species-level invertebrate systematics. The purpose of this paper is to describe a new species of columbellid gastropod, *Columbella moinensis*, that differs from another Caribbean *Columbella* species in its inferred developmental mode. Additionally, the 2 species appear to be allopatric, lending further support to their taxonomic distinction.

Columbella Lamarck, 1799 is primarily a tropical American taxon, consisting of 15 Neogene and Recent American species and 2 species in the eastern Atlantic. Phylogenetic analyses of representative columbellid taxa (deMaintenon, 1999) supports the monophyly of *Columbella*, based on 8 characters of anatomy, radular morphology and shell morphology. Recent species of *Columbella* are differentiated primarily on the basis of conchological characters. The extant species comprise 2 morphological groups, one of which occurs in the Atlantic. The Atlantic *Columbella* species are very similar, and are characterized by having shells with spiral cords over the entire shell surface. They differ primarily in shell coloration and in the number and strength of spiral cords. Jung (1994) recently reviewed the fossil species of the Atlantic group in a discussion of the *Columbella* species from the Neogene of the Dominican Republic. The extant members of the Atlantic group include 2 species in the eastern Atlantic and 2 in the western Atlantic. The known fossil record of the group extends back to the late Miocene. Of the living and fossil species of *Columbella* in the Atlantic, the new species is the only one considered to have planktic development.

The second group comprises the 10 extant Panamic *Columbella* species. These differ from the Atlantic group by lacking spiral cords on the shell except as juveniles. All members of the Pacific group have multiwhorled protoconchs, and are inferred to have planktic development. The fossil record of this group is unknown before the Pliocene, when the extant species appear. Allopatric species pairs differing in developmental mode already have been reported in the group of Atlantic *Columbella* species. Moolenbeek and Hoenselaar (1991) differentiated 2 species in the eastern Atlantic: *Columbella rustica* (Linnaeus, 1758) with nonplanktic development, in the Mediterranean and eastern Atlantic coast, and *Columbella adansoni* (Menke, 1853) with planktic development, endemic to the offshore islands of the eastern Atlantic. Study of allozyme data from these 2 species (Oliverio, 1995, 1996) indicates that they diverged about 2 million years ago. The new species described herein has a similar relationship with one of the western Atlantic species, *Columbella mercatoria* (Linnaeus, 1758).

The following institutional abbreviations are used: UF, University of Florida, Florida Museum of Natural His-

tory; SBMNH, Santa Barbara Museum of Natural History; UCMP, University of California Museum of Paleontology; USGS, United States Geological Survey; USNM, National Museum of Natural History, Smithsonian Institution.

The micrographs in figures 1 and 2 were taken using the Electroscan Environmental Scanning Electron Microscope at the University of California Museum of Paleontology. Specimens were scanned uncoated, at 15 kV and between 2 and 3 Torr water vapor.

SYSTEMATICS

Family Columbellidae Swainson, 1840
Genus *Columbella* Lamarck, 1799

Columbella moinensis new species
(Figures 2, 4–8, Table 1)

Description: Shell small, strombiform, up to 19 mm shell length. Aperture length slightly more than half shell length. Protoconch conical, multiwhorled, smooth, with 3 whorls. Teleoconch with 6–7.5 whorls, with spiral cords over all whorls. Body whorl with 12–18 cords counted at the aperture edge, continuing anteriorly to a few finer cords at the base of the shell. Each spire whorl with 4–6 cords visible. Usually with a prominent, slightly nodulose cord at the shoulder, which is most often the second cord below the suture. First 2–3 teleoconch whorls with nodules at the periphery and weak axial ridges, which fade out on subsequent whorls. Aperture constricted by inrolled labial edge, thickest in the center. Labial edge with 10–12 denticles, facing inward. Columella with 2 weak folds. Anterior parietal wall with 5–10 denticles in an axial row. Short posterior parietal callus, continuous with aperture edge.

Type material: Holotype, UCMP 39918, 12.8 mm long, 7.5 mm wide, type locality. Paratype UCMP 39919, type locality; Paratypes UCMP 39920 and 39921, Upper Tubará Group, below type locality, Punta Pua, Bolivar, Colombia; Paratype USNM 501150, Moín Fm. 2 km west of Puerto Limon, Costa Rica; Paratype USNM 501151, Moín Formation, between Puerto Limon and Pueblo Nuevo, Costa Rica.

Type locality: Upper Tubará Group, Punta Pua, about 15 miles northeast of Cartagena, Bolivar, Colombia (UCMP S-66).

Other material examined: USGS locality 21037, 1 specimen, Moín Formation, outskirts of Puerto Limon, Costa Rica; UCMP S-66, 11 specimens; UCMP S-65, 2 specimens; TU 954, 1 specimen; TU 956, 1 specimen.

Distribution: The known lots of *Columbella moinensis* are from the Pliocene to Pleistocene (?) of Costa Rica and Colombia. The material from Colombia lacks precise stratigraphic data but is thought to be from the Miocene to Pliocene Tubará Group (Vokes, 1990). Vokes (1990) reported that the muricid species she studied from these 2 Colombian localities are typical of the Pleistocene Moín fauna from Costa Rica. Although the Moín Formation has better stratigraphic definition than the above mentioned units, some controversy exists about the age of the formation. Coates *et al.* (1993) state that the Moín Formation is Late Pliocene in age, however its faunas are more usually considered to be Pleistocene in age (Robinson, 1993, and references therein). Thus the stratigraphic range of this species is currently imprecise.

Etymology: *Columbella moinensis* is named after the Moín Formation of Costa Rica.

Discussion: *Columbella moinensis* is very similar to *Columbella mercatoria* (Linnaeus, 1758) (Figure 3), a common western Atlantic species known from the Pliocene to the Recent. The new species can be differentiated from *C. mercatoria* by its multiwhorled protoconch. *Columbella mercatoria* has 1.5 to 2 bulbous protoconch whorls (Figure 1), with at least one specimen having 2.25 whorls. The new species has a conical protoconch with 3 whorls (Figure 2), and its nuclear whorl is smaller than that of *C. mercatoria*. This latter species has nonplanktic development; its eggs hatch as crawling juveniles after about 33 days, during which the larvae feed on nurse eggs in the capsules (Bandel, 1974). The multiwhorled protoconch of *C. moinensis*, in contrast, is indicative of planktic development.

Columbella mercatoria varies greatly in adult size and strength of sculpturing, as do many other *Columbella* species. In the case of *C. mercatoria*, this variation may be a function of environment. In southern Florida, the species is commonly associated with both reef rock and seagrass habitats, and specimens found in seagrasses tend to be smaller and less brightly patterned than reef specimens. The known specimens of *C. moinensis* come from only 6 lots, and most of the material is similar in size. The single specimen from USGS locality 21037 (USNM 501152, Figure 8) is markedly larger than other specimens (Table 1), and has a weaker shoulder. It does have a multiwhorled protoconch (broken off though still with the shell) consistent with that of *C. moinensis*, so will be referred to the new species in spite of the differences between it and other specimens.

Many of the specimens that are considered to represent *C. moinensis* have eroded protoconchs and thus cannot be diagnosed with certainty. However, they are comparable in shape and size to specimens of *C. moinensis* from the same localities.

Columbella mercatoria was contemporaneous with *C. moinensis*. However, the 2 species have not so far been found sympatrically. *Columbella mercatoria* has been collected in the Pliocene and Pleistocene Mare and Abisinia Formations of Venezuela (Weisbord, 1962) and in the Pliocene Bowden Formation of Jamaica (a worn and damaged specimen incorrectly identified as *Columbella submercatoria* is illustrated by Woodring, 1928).

Columbella submercatoria Olsson, 1922 occurs in the Late Miocene of the Dominican Republic (Jung, 1994)

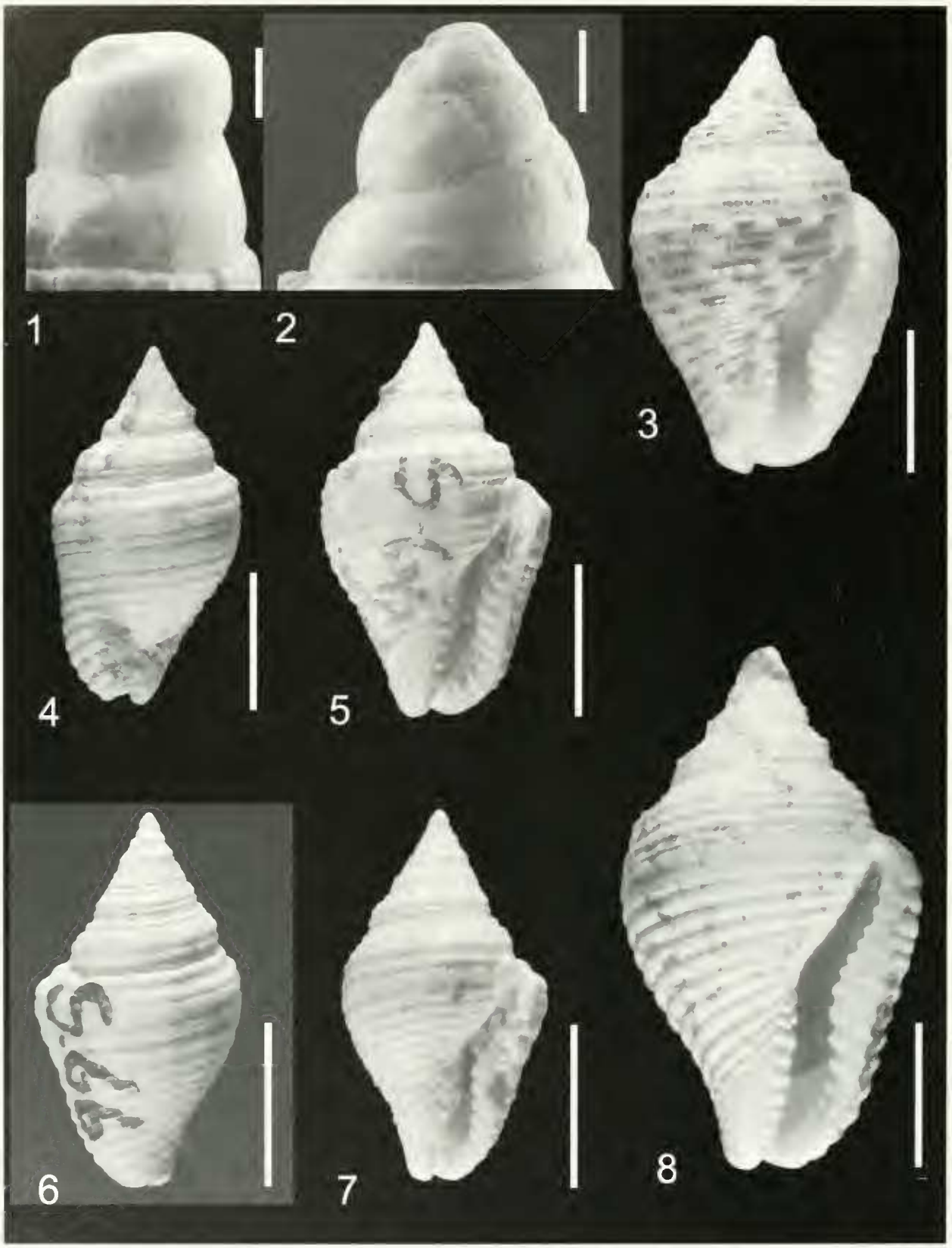

Figure 1. Recent *Columbella mercatoria*, protoconch, UF 126820, Colon Island, Bocas del Toro Province, Panama. Scale line = 200 μm. **Figure 2.** *Columbella moinensis* new species. Protoconch of paratype, UCMP 39919. Scale line = 200 μm. **Figure 3.** Recent *Columbella mercatoria* (SBMNH 144851, Los Totumos, Venezuela). Scale line = 5 mm. **Figures 4–5.** *Columbella moinensis* new species. Holotype, UCMP 39918. Scale line = 5 mm. **Figures 6–7.** *Columbella moinensis* new species. Paratype, UCMP 39919. Scale line = 5 mm. **Figure 8.** Large specimen of *Columbella moinensis* new species, USNM 501152. Scale line = 5 mm.

Table 1. Lengths and widths in mm, and number of cords on the body whorl of types and figured specimens.

Specimen	Max. length (mm)	Max. width (mm)	No. of spiral cords
Holotype, UCMP 39918	12.8	7.5	14
Paratype, UCMP 39919	11.4	6.3	14
Paratype, UCMP 39920	15.3	8.7	12
Paratype, UCMP 39921	15.8	9.1	17
Paratype, USNM 501150	10.1	5.5	15
Paratype, USNM 501151	12.5	7.2	16
USNM 501152	18.6	10.4	17

and in the Neogene of Costa Rica. Whether this is a distinct species or a form of *C. mercatoria* has been debated and should still be regarded as uncertain. The primary difference between them is the greater number of spiral cords on *C. submercatoria* (22 to 25 per whorl rather than 15 to 20), but large specimens of extant *C. mercatoria* from some areas of the Caribbean also have a greater number of spiral cords than usual. The type locality for *C. submercatoria* is Red Cliff Creek, Costa Rica, a locality that is presently unlocated but thought to correspond to late Miocene or early Pliocene beds in the Limon Basin (Jung, 1994). *Columbella submercatoria* has a paucispiral protoconch of about 1.5 whorls (Jung, 1994), similar to that of *C. mercatoria*.

LITERATURE CITED

Bandel, K. 1974. Spawning and development of some Columbellidae from the Caribbean Sea of Colombia (South America). The Veliger 16:271–282.

Bouchet, P. 1989. A review of poecilogony in gastropods. Journal of Molluscan Studies 55:67–78.

Coates, A. G., J. B. C. Jackson, L. S. Collins, T. M. Cronin, H. J. Dowsett, L. M. Bybell, P. Jung, and J. A. Obando. 1992. Closure of the Isthmus of Panama: the near-shore marine record of Costa Rica and western Panama. Bulletin of the Geological Society of America 104:814–828.

Jung, P. 1994. Neogene paleontology in the Northern Dominican Republic 15. The genera *Columbella, Eurypyrene, Parametaria, Conella, Nitidella*, and *Metulella* (Gastropoda: Columbellidae). Bulletin of American Paleontology 106(344):1–45.

deMaintenon, M. 1999. The phylogenetic relationships of modern columbellid taxa (Neogastropoda: Columbellidae), and the evolution of herbivory from carnivory. Invertebrate Biology 118:258–288.

Hoagland, K. E. and R. Robertson. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? Biological Bulletin 174:109–125.

Knowlton, N. 1993. Sibling species in the sea. Annual Review of Ecology and Systematics 24:189–216.

Moolenbeek, R. G. and H. J. Hoenselaar. 1991. On the identity of '*Columbella rustica*' from West Africa and the Macaronesian Islands. Bulletin Zoölogisch Museum 13:65–70.

Oliverio, M. 1995. Larval development and allozyme variation in East Atlantic *Columbella* (Gastropoda: Prosobranchia: Columbellidae). Scientia Marina 52:77–86.

Oliverio, M. 1996. Life-histories, speciation, and biodiversity in Mediterranean prosobranch gastropods. Vie et Milieu 46: 163–169.

Robinson, D. G. 1993. The zoogeographic implications of the prosobranch gastropods of the Moín Formation of Costa Rica. American Malacological Bulletin 10:251–255.

Weisbord, N. E. 1962. Late Cenozoic gastropods from Northern Venezuela. Bulletin of American Paleontology 42(193):1–672.

Woodring, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part 2: gastropods and discussion of results. Carnegie Institute of Washington. 564 pp., 40 pls.

Vokes, E. 1990. Cenozoic Muricidae of the West Atlantic region Pt. VIII—*Murex* s.s., *Haustellum, Chicoreus* and *Hexaplex*; additions and corrections. Tulane Studies in Geology and Paleontology 23:1–96.